

The role of signature whistle matching in bottlenose dolphins, *Tursiops truncatus*



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The addressing of individuals with learned signals is inherent to human social interactions. It allows individuals to solicit the attention of a particular social companion or to direct information towards an intended recipient. The ability to address individual conspecifics with learned signals is not limited to humans, however. In songbirds, the selective addressing of individuals is facilitated by song type matching but is very much a signal of aggressive intent. The matching of learned signals is also observed in bottlenose dolphins, which will match one another's highly individualized signature whistle. Copying in dolphins occurs between close associates, which suggests that it is an affiliative signal. It could, however, also serve to manage aggression. We investigated the valence of signature whistle matching by performing interactive playback experiments. We waited until an animal produced its signature whistle and then either played back a synthetic version of its own whistle (match) or a different signature whistle (control). A total of 110 playback experiments were conducted with seven different animals from two managed groups of dolphins. The responses to the playback treatments were significantly different. Animals produced a consistent vocal response to being vocally matched, by returning the match, with no associated signal of aggression and did not respond to control playbacks in the same way. There was also an optimum time interval (<1 s) in which a match was most successful in eliciting a vocal response. Our results show that signature whistle matching is an affiliative signal that allows bottlenose dolphins to address social companions. Furthermore, these matching exchanges are driven by temporal associations, which appear to be essential in allowing animals to direct signals to particular individuals in large communication networks.

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Vocal matching with learned signals is a powerful mode of interaction utilized by a select number of animals, namely songbirds (Searcy & Beecher, 2009), parrots (Balsby & Bradbury, 2009; Balsby, Momberg, & Dabelsteen, 2012) and odontocetes (Janik, 2000; King, Sayigh, Wells, Fellner, & Janik, 2013; Miller, Shapiro, Tyack, & Solow, 2004; Schulz, Whitehead, Gero, & Rendell, 2008). Matching can be described as a receiver responding to a signal by changing some features of its own vocal behaviour in order to imitate the preceding signal. The rapid matching of acoustic signals is a way of directing a response towards an intended receiver thus allowing a signaller to address individual conspecifics. Theory predicts that it should be common in complex communication networks in which signals can be directed at a multitude of listeners (McGregor & Dabelsteen, 1996).

The timing of the response is a crucial factor in vocal matching. A rapid response may be perceived as an aggressive act (Beecher, Campbell, Burt, Hill, & Nordby, 2000; Searcy & Beecher, 2009), whereas a long interval between signals may not be seen as a response to the first signal. Studies on a variety of species show that, in general terms, the timing of call production appears to be governed by temporal rules whereby animals reply to a signal within a short time interval (Kureta, 2000; Masataka & Biben, 1987; Nakahara & Miyazaki, 2011; Sugiura, 1993). For example, in nightingales, *Luscinia megarhynchos*, response latencies in vocal matching interactions are much shorter when song types are matched than when they are not (Geberzahn, Hultsch, & Todt, 2013). Geberzahn et al. (2013) suggested that memory of song patterns may influence the response latencies.

The duration of the interval until a matching response is given may also indicate the motivation of the respondent (Todt, 1981; Todt & Naguib, 2000). Todt (1981) considered both overlapping matching and delayed matching (where an animal waits until after

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the signaller has called), with the former hypothesized to be a 'vocal threat' or agonistic in nature as it was associated with high arousal, and the latter as a more affiliative exchange or 'vocal greeting' as it seemed to occur when birds were less aroused (Todt, 1981; Todt & Hultsch, 1996). Overlapping of the same signal type between two individuals occurs in highly escalated vocal contests in some bird species (McGregor, Dabelsteen, Shepherd, & Pedersen, 1992; Vehrencamp, 2001) and may be seen as an extension of rapid matching and therefore agonistic in nature (Naguib & Mennill, 2010). This vocal behaviour does not, however, appear to occur above chance levels and therefore the functional significance of overlapping remains an area of contention (Naguib & Mennill, 2010; Searcy & Beecher, 2009, 2010). Furthermore, overlapping can be found in duetting birds as an affiliative signal (Hall, 2009). In contrast, if a respondent delays a vocal match until after the signaller has called then vocal interference is avoided and more subtle information, encoded in the calls, can be exchanged between the individuals (Todt & Naguib, 2000). As such, the signal value of matching is closely linked to the temporal interval of the response.

To date, vocal matching has been best studied in songbirds; male song sparrows, *Melospiza melodia*, for example, can reply to the song of another male by singing the song type in their repertoire that most resembles it, known as song type matching (Searcy & Beecher, 2009). This matching of vocal signals appears to be an honest signal of aggressive intent (Akçay, Tom, Campbell, & Beecher, 2013; Beecher et al., 2000; Burt, Campbell, & Beecher, 2001; Searcy & Beecher, 2009). Male songbirds may identify one another by becoming familiar with each other's learned song repertoire via location of territories or fine-scale differences between individuals in shared song types (Falls, 1982; Falls & Brooks, 1975; Nordby, Campbell, & Beecher, 2007; Stoddard, Beecher, Horning, & Campbell, 1991). This then allows individuals to choose the song from their repertoire that most closely matches that of the male they wish to address (McGregor & Dabelsteen, 1996; McGregor et al., 1992). This does, however, mean that a male's ability to partake in song type matching may be somewhat limited to the song types it has in its vocal repertoire. Other species, such as orange-fronted conures, *Aratinga canicularis*, and bottlenose dolphins may be less constrained by their repertoire in matching interactions (Balsby et al., 2012; Janik, 2000; King et al., 2013; Tyack, 1991).

The evolution of learned, individually distinctive calls in dolphins is most likely to be linked to their fluid social network and their high mobility coupled with features of the marine environment (i.e. pressure affecting subtle voice features and restricted vision underwater; Janik, 1999; Tibbetts & Dale, 2007). The individual identity of each animal is encoded in the frequency modulation pattern of these whistles independently of general voice features (Janik, Sayigh, & Wells, 2006). Thus, each animal's signature whistle may become a label for that particular individual and conspecifics can then use these learned labels to address one another (King & Janik, 2013). The copying of signature whistles in this way appears to be an affiliative signal that primarily occurs between animals that share strong social bonds (King et al., 2013). Signature whistle copies can also occur in matching interactions (Janik, 2000; King et al., 2013). It is unclear whether this means all such interactions are affiliative or whether they can also serve to manage aggression as seen in songbirds (Searcy & Beecher, 2009).

We investigated how bottlenose dolphins responded to being vocally matched by conducting playback experiments with groups of animals under human care. We waited until an animal produced its signature whistle and then played either a synthetic version of its own whistle (match) or a different signature whistle (control). Following the addressing theory of whistle copying, we hypothesized that signature whistle matching would elicit responsive calling in the target animal but that different signature whistles

would not. To investigate the valence of matching we explored the role of the timing of the match and noted potential signs of aggression such as approaches and threat displays.

METHODS

Study Subjects

Playback experiments were conducted at two facilities: Walt Disney World's Epcot's The Seas in Kissimmee, FL, U.S.A. during May–June 2009 and Dolphin Quest, Bermuda during February–March 2011. The subjects from The Seas were four adult male bottlenose dolphins. Ranier was 28 years old, born in the Gulf of Mexico, and had lived in multiple facilities before coming to The Seas in 2002. The other males were Khyber (18 years), Calvin (15 years) and Malabar (8 years), all born in human care. All four animals had been together for the previous 3.5 years, Ranier and Calvin for 6 years. The dolphins were housed in an indoor facility and usually kept in pairs, with one pair in the main pool (20 318 m³ cylindrical pool with a diameter of 28 m and a depth of 8.2 m) and the second pair in two interconnected back pools that could be separated from the main pool by two watertight gates. The playbacks occurred in the two back pools, which were each approximately 100 m³ (56 m² in area with a 2 m depth). The animals had constant acoustic contact but only had visual contact through one of the gates during playback sessions. Vocalizations at The Seas were recorded with two HTI-96 MIN hydrophones (frequency response: 0.002–30 kHz $\pm$ 1 dB) and two CRT hydrophones (C54XRS; frequency response: 0.016–44 kHz, C54XR $\pm$ 3 dB; frequency response: 0.016–50 kHz $\pm$ 3 dB) onto a Toshiba Satellite Pro laptop using a four-channel Avisoft 416 UltrasoundGate recording device (sampled at 50 kHz, 8 bit; frequency response: 0.02–25 kHz $\pm$ 3 dB). Passive acoustic localization was used to identify the caller, by comparing the amplitude of the same sound recorded on four hydrophones placed in different areas of the pools (Janik & Slater, 1998). Video recordings were taken using two digital video cameras mounted above the back pools and from a third analogue VN37CPH underwater camera attached to a Sony Handycam DCR-HC96E and recorded onto mini DV tapes. The Sony Handycam also had an acoustic input from one of the HTI-96 MIN hydrophones.

The subjects from Dolphin Quest Bermuda were four adult females and three calves. Cirrus was 37 years old and was born in the Gulf of Mexico; she was the only female without a calf at the time of study. Both Bailey (22 years old) and Caliban (18 years old) were born in human care and all three of these females had been housed together at Dolphin Quest for the last 15 years. The fourth adult female was Ely (8 years old), and she was born at the facility to Bailey. The three calves were all 11 months old at the time of study. The two female calves were Cavello (calf of Bailey) and Marley (calf of Ely); the male calf was Cooper (calf of Caliban). The animals were kept in outdoor tidal pools with a floating dock, and therefore had both constant acoustic and visual contact. The animals were kept in different group compositions that changed on a daily basis. The playback pool was 120 m² in area with depth dependent on tide and varied across pool area (range 1–7 m). Vocalizations of the animals at Dolphin Quest were recorded with four HTI-96 MIN hydrophones (frequency response: 0.002–30 kHz $\pm$ 1 dB) onto a Dell laptop using the same Avisoft 416 UltrasoundGate described above. Whistles were localized to an individual using the TOADY localization program (Quick, Rendell, & Janik, 2008). Video recordings were taken from an analogue VN37CPH underwater camera attached to a Sony Handycam DCR-HC96E and recorded onto mini DV tapes. The Sony Handycam also had an acoustic input from one of the HTI-96 MIN hydrophones.

Experimental Playback

Sounds were played back through a Lubell LL916 underwater speaker (Lubell Labs Inc, Columbus, OH, U.S.A.; frequency response: 600 Hz–21 kHz $\pm$ 8dB) connected to a Magnat classic 1000 XL car amplifier (frequency response: 0.005–100 kHz $\pm$ 3 dB). Stimuli were played back from a Toshiba Satellite Pro laptop using the Avisoft 416 Ultrasoundgate with Avisoft RECORDER v3.4 (Avisoft Bioacoustics; frequency response: 0.02–25 kHz $\pm$ 3 dB). The source level of the playbacks conducted at both facilities was 121 $\pm$ 5 dB re 1 μ Pa (rms) at 1 m. The source level was measured with a calibrated Reson TC 4013 hydrophone, a Reson VP 1000 voltage preamp and a Tucker-Davis Technologies RX6 multifunction processor. Sound acquisition was on a Dell laptop using MatLab. In both facilities the speaker was kept in the same location for all sound playback experiments.

Playback Stimuli

The signature whistles of the target animals were identified by recording the most common whistle produced by the animal when isolated from group members (Caldwell, Caldwell, & Tyack, 1990). All of the whistles used as stimuli in the playbacks were synthetic versions of signature whistles using SIGNAL v 4.0 for synthesis (Engineering Design, Berkeley, CA, U.S.A.; see method in Janik et al., 2006). The control treatment could be either unfamiliar or familiar signature whistles. Unfamiliar signature whistles were used from eight different wild animals (six males and two females) from the Sarasota Dolphin Whistle Catalogue (Sayigh, Esch, Wells, & Janik, 2007) and from one adult female bottlenose dolphin from Zoo Duisburg, Germany (Janik & Slater, 1998). Familiar signature whistle controls consisted of the signature whistle of a nontarget animal from the same managed group as the target animal; they were incorporated for 11 playbacks to three different animals (one from The Seas; two from Dolphin Quest).

Playback Protocol

Vocalizations of animals were monitored in real-time on spectrograms produced by Avisoft RECORDER to allow us to time the playback correctly. We waited until the target animal produced its signature whistle, at which point we either simulated a vocal match by playing back a synthetic version of the animal's own signature whistle (the same whistle pattern) or played back a control, the synthetic signature whistle of either a familiar or an unfamiliar

animal (different whistle pattern). A temporal parameter was also incorporated in the design by introducing different time delays between the target animal producing its signature whistle and the start of the playback. The time delays ranged from overlapping the target animal to producing the playback up to 13 s after the target animal produced its signature whistle. Whistle overlap was difficult to achieve resulting in only a small proportion of the whistles being overlapped. If another animal vocalized before we played the matching whistle or control whistle then the trial was not included in further analyses. The playback treatments were randomized in their playback sequence and were conducted when the animals were not involved in activities with their trainers. Playbacks were only included in the analysis if the vocalizations produced in response to the playback could be localized to the target animal.

Eliciting Whistles

Playbacks of signature whistles from other pool members were used in some trials to elicit signature whistle calling in the target animal. This helped to increase the sample size of playbacks as the animals often remained quiet for extended periods of time. Since signature whistle use in one animal often coincides with the calling of conspecifics, we used playbacks of the signature whistle of one of the nontarget animals from the same facility to initiate signature whistle calling in the target animal (Fig. 1). The nontarget stimulus was produced up to seven times over a 30 s period. Upon the target animal producing its signature whistle the playback of the nontarget animal was ceased and one of the playback treatments was played.

The four adult males in The Seas were predominantly quiet and so the playback designed to elicit whistles was employed for nearly every trial. Only two of the four males responded to the pool-mate playbacks (in which a signature whistle of a nontarget pool member was played) and produced their own signature whistles. The seven bottlenose dolphins at Dolphin Quest were more vocal than those at The Seas and playbacks were largely conducted when the animals vocalized spontaneously (Fig. 1).

Data Analysis

Responses to playbacks were analysed by inspecting the spectrograms (FFT length 1024, overlap 100%, Hanning window) in Adobe Audition v2.0 (Adobe Systems). All statistical procedures were conducted in R (The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org>; GNU project). The

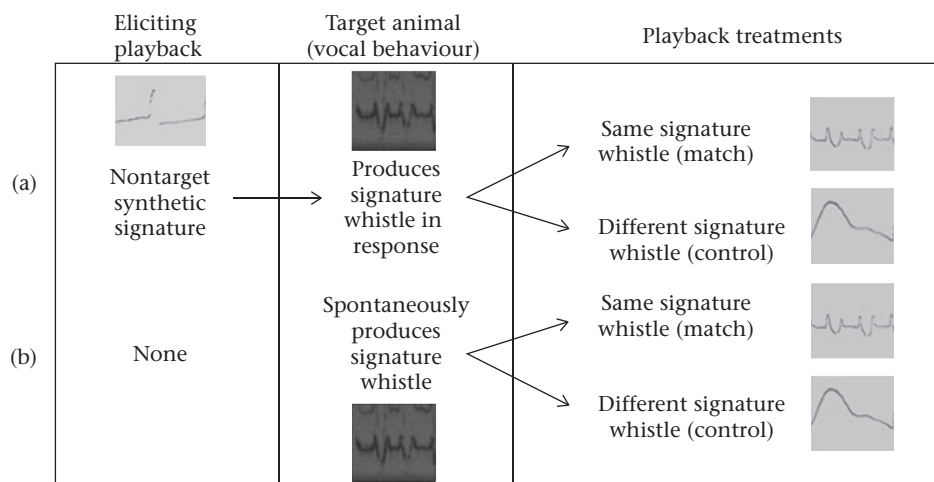


Figure 1. Playback experiments conducted during this study followed either protocol (a) in which playbacks of signature whistles from other pool members were used to elicit signature whistle calling in the target animal, or (b) the playback was conducted when the animal vocalized spontaneously.

animals' vocal responses to the different treatments in the 1 min after playback were recorded. We used a generalized linear mixed-effects model (GLMM) with a binomial family (GLMER using lme4 package in R software version 3.0.2; Bolker et al., 2009) to assess the initial vocal response given to the playback treatments. The type of vocal response (signature whistle = 1, no whistle or non-matching whistle = 0) was treated as the binary response variable. The playback treatment and the time delay that was incorporated between playbacks were included as fixed effects. To account for the fact that playback experiments were repeated across individuals, we included animal identity as a random effect. Forward model selection was performed using ANOVA with a *P* value significance level of 0.05. An interaction term between animal identity and treatment was also incorporated to explore the relationship between individual responses to playback treatments. A model with a random intercept but no random slope (i.e. no interaction with fixed effects) was preferred by the Akaike information criterion (AIC).

Animals are known to adjust fine-scale parameters of their calls as a result of changes in their motivational state (Janik, Dehnhardt, & Todt, 1994) or to encode additional information (Biben, Symmes, & Masataka, 1986). We therefore compared the target animal's signature whistle before and after the vocal match playback to see whether the animals adjusted fine-scale temporal or frequency parameters of their signature whistle as a result of the match. The signature whistle contours (frequency modulation pattern) were extracted using a supervised contour extraction program (Deecke & Janik, 2006). The whistle contours had a time resolution of 5 ms and the following parameters were measured: start frequency, end frequency, minimum frequency, maximum frequency and duration. The number of loops was also measured; a loop was defined as a repeated modulation pattern within a signature whistle that could be separated by periods of stereotyped silence of up to 250 ms (Esch, Sayigh, & Wells, 2009). A pairwise comparison was performed for each of the parameter measurements taken from the target animal's signature whistle before and after the match playback. An *F* test to compare variances was conducted followed by a paired *t* test.

The behavioural responses to the matching and control playback trials were compared in order to ascertain whether animals adjusted their behaviour in response to being vocally matched. The following continuous variables were measured: time (s) spent in the playback pool, time (s) spent in a different pool, time (s) spent within 3 m (one body length) of the playback speaker, time (s) spent at more than 3 m (one body length) of the playback speaker (in the playback pool). Swim speed was also measured (see Appendix 1). All measurements were taken during a 1 min period after playback. Owing to the strong correlation between variables, a principal component analysis was used to derive a single composite behavioural response score (McGregor, 1992). Seven outliers (10% of the data) were identified using Mahalanobis distance and were removed to achieve multivariate normality. The first two component factors accounted for 91% of the variance and were used to calculate the behavioural response scores. A two-tailed Wilcoxon rank sum test was used to test whether animals responded differently to the two playback treatments. The presence or absence of immediate behavioural reactions (jaw clapping, tail slapping and repeated burst pulsed sounds) was also noted in order to ascertain whether vocal matching induces aggressive states (Overstrom, 1983) as can occur with type matching in songbirds.

RESULTS

We conducted 110 playback experiments with seven different individuals from the two groups (Table 1). Of these, 61 were own

Table 1

The study animals with the number of playback experiments to which they were subjected for the two different signature whistle (SW) treatments, own (vocal match) and different (control)

	Sex	Age	Playback treatments	
			Own SW (match)	Different SW (control)
Ranier (The Seas)	Male	28 years	18 (17)	17 (4)
Khyber (The Seas)	Male	18 years	4 (4)	2 (0)
Cirrus (DQ Bermuda)	Female	37 years	16 (16)	12 (7)
Bailey (DQ Bermuda)	Female	22 years	10 (6)	11 (1)
Caliban (DQ Bermuda)	Female	18 years	3 (0)	0
Cooper (DQ Bermuda)	Male	11 months	7 (2)	5 (0)
Cavello (DQ Bermuda)	Female	11 months	3 (2)	2 (0)

The number of times the animals replied to the playbacks with their signature whistle is provided in parentheses.

signature whistle (vocal match) playbacks and 49 were different signature whistle (control) playbacks (Table 1).

At The Seas, 99 initial whistle playbacks were conducted over 28 days to elicit signature whistle calling in two adult males (Khyber and Ranier). These playbacks elicited 34 vocal responses from Ranier and six from Khyber and a vocal match or control playback followed each (Table 1). One additional playback was conducted with Ranier when he called spontaneously. On average 3.4 (range 2–6) match or control playback experiments were conducted on a given day with a trial lasting on average 7.8 min (range 3–28). The average latency between the initial nontarget animal stimulus whistle and a target animal's matching response was 0.56 s (range 0–2.9). The mean number of stimulus whistles played back to the target animals in order to elicit a signature whistle response was 2 (range 1–7). At Dolphin Quest, a total of 69 successful playbacks were conducted over 16 days to five different target animals (Table 1). Only 11 of these playbacks involved a playback component that used a nontarget animal's signature whistle as a stimulus. On average 9.1 (range 2–22) playback trials were conducted on a single day and the average duration of a playback session was 1 h 25 min (range 42 min–3 h 22 min).

Did Animals Respond to Being Vocally Matched?

The type of vocal response given to the two different playback treatments was significantly different (GLMM: $\chi^2_4 = 40.9$, $P < 0.0001$; Fig. 2). The results revealed that the vocal response of an animal being vocally matched by its own signature whistle (the whistle it had just produced) was to reciprocate the match by producing its signature whistle again, and that this was significantly different to the response of the animal when a different signature whistle (control) was played (Figs 2, 3). No difference was found in the type of vocal response given to the two different types of signature whistle controls: familiar ($N = 12$) versus unfamiliar ($N = 37$) signature whistles (Fisher's exact test: $N = 49$, $P = 1$). Animals did not respond to the control treatments by matching the control stimuli (Fig. 3). They were mostly silent, occasionally producing their signature whistle or a nonsignature whistle.

We also found a significant decrease in vocal response (GLMM: $\chi^2_4 = 4.7$, $P = 0.03$; Fig. 4) as time between the animal vocalizing and the playback increased. There was a clear pattern with the animal nearly always responding to a playback of its own signature whistle (match) when it occurred within 1 s after the animal vocalized. The average latency between the playback match and the animal's response was 0.68 s (range 0.01–5). There was also a slight increase in vocal responses to the playbacks of a different signature whistle (control) within the same time period. There, therefore, seems to be an optimum time frame in which a match elicits a

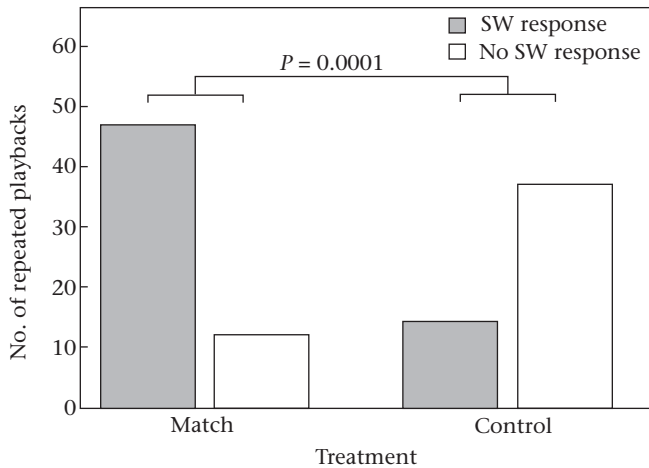


Figure 2. The vocal response of the seven bottlenose dolphins to being vocally matched by either their own signature whistle (match) or a different signature whistle (control) using a repeated measures playback design. The vocal response is either that the target animal produces its signature whistle (grey) or that it produces no response or another vocalization (white).

response (<1 s), above which there is a decline in response strength.

There was no evidence that the animals were adjusting the acoustic parameters of their signature whistles as a result of being vocally matched (see [Appendix 2](#)). They were therefore not adjusting their signature whistle to more closely match or deviate from the playback whistle. The behavioural responses of the animals did not differ to the two playback treatments (response score 1: Wilcoxon rank sum test: $W = 400$, $N_1 = 27$, $N_2 = 35$, $P = 0.3$; response score 2: $W = 562$, $N_1 = 27$, $N_2 = 35$, $P = 0.2$; principal component scores are provided in [Table 2](#)). We observed no behavioural reactions aligned with aggressive behaviour such as jaw popping, tail slapping or repeated production of loud, intense vocalizations. We also found no evidence that overlap matching was an aggressive signal.

DISCUSSION

We have shown, with the use of interactive playback, that bottlenose dolphins produce a consistent vocal response to being vocally matched, by returning the match, with no associated signal of aggression. Thus, matching of signature whistles clearly allows the matching individual to address the caller. The eliciting playback approach, whereby the whistle of a nontarget male was played first, was effective at initiating signature whistle calling in the target animals. This study therefore provides further support for interactive playback being a powerful tool in the study of animal communication.

Given that signature whistles are often produced in repetitive sequences ([Janik, King, Sayigh, & Wells, 2013](#)), there is the possibility that instead of responding to being vocally matched, animals were just continuing their signature whistle sequence. The most common interwhistle interval between signature whistles of the same type in wild animals is 5–10 s ([Janik, King, Sayigh, & Wells, 2013](#)). However, in two Japanese aquaria, interwhistle intervals of signature whistle sequences have been reported to be between 1 and 5 s ([Nakahara & Miyazaki, 2011](#)). Given the close proximity of animals to each other in their and our study, the latency between calls, i.e. the time given for a receiver to respond, may be shorter owing to the short signal transmission distance. In those trials when the match was delayed by greater than 5 s (range 6–13 s), our target animals remained quiet (after initially producing their signature whistle) until the match was played and then still responded to the match by replying with their signature whistles ([Fig. 4](#)). In addition, sequences of signature whistles were not frequently produced in either facility during the recording period, probably because the animals were either quiet (The Seas) or were in constant visual contact (Dolphin Quest) negating the need for call redundancy. It is therefore unlikely that the vocal responses to the match playbacks were a result of repetitive calling but instead are direct responses to being matched.

None of the animals ever responded by matching the control playbacks (different signature whistles). This is not, however, because of a lack of ability to do so. Bottlenose dolphins are known to copy the signature whistles of social companions ([King et al.,](#)

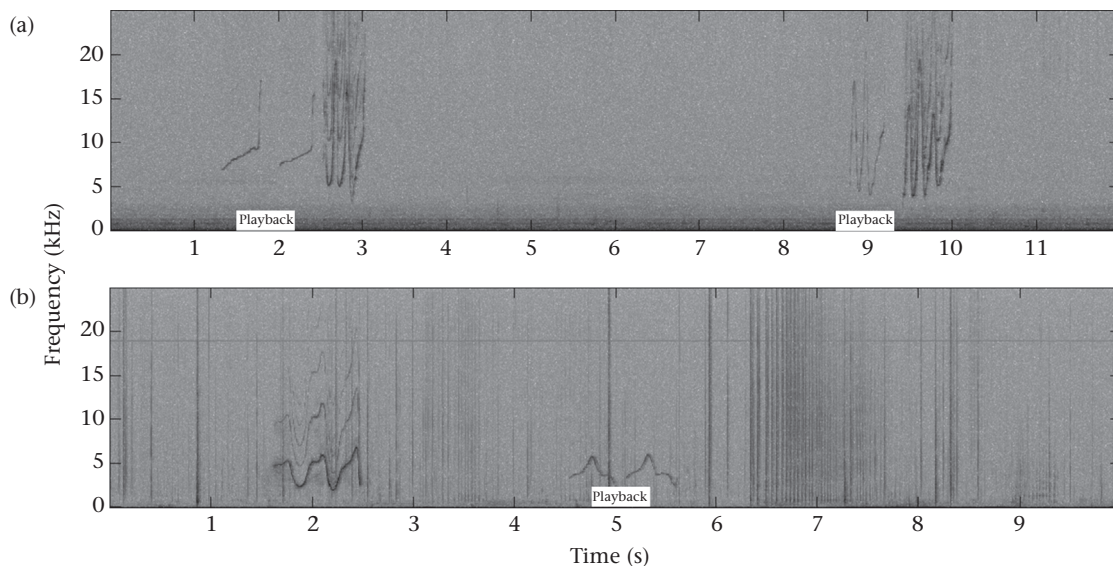


Figure 3. Spectrograms showing examples of (a) an eliciting playback followed by a matching playback with the adult male Ranier at The Seas in which Ranier replied with a match, and (b) an unfamiliar control playback with the adult female Bailey at Dolphin Quest in which Bailey did not respond. Sampling rate is 48 000 Hz, FFT length 1024, Hanning window function. The playback stimuli are highlighted with the label 'Playback'.

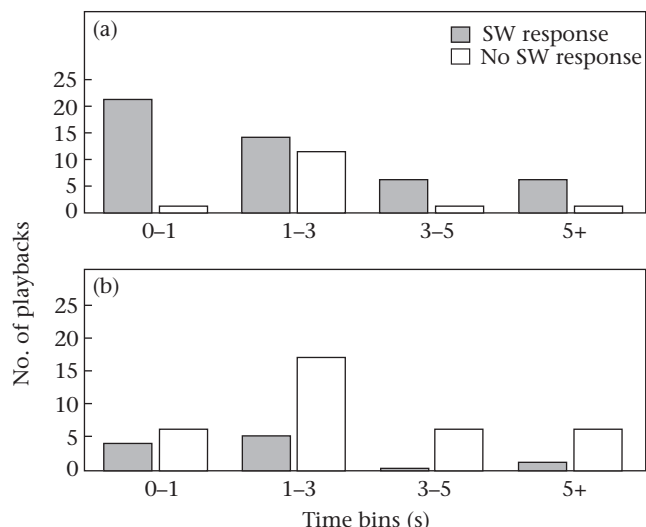


Figure 4. The vocal response of the seven animals to being vocally matched by either (a) their own signature whistle or (b) a different signature whistle at varying lengths of time after they produced their own signature whistle. The vocal response is either the target animal producing its signature whistle (grey) or there was no response or another vocalization (white).

2013) so they certainly have the ability to copy our familiar control signature whistles. They are also adept vocal mimics and can produce almost perfect copies of novel acoustic signals after only one exposure (Richards, Wolz, & Herman, 1984). It is therefore highly likely they are able to copy the signature whistle of a stranger (unfamiliar control whistles).

There appears to be an optimum time interval (<1 s) in which a match should occur in order to reliably elicit a vocal response, after which there is a decline in response strength. The average time for an animal to respond to the match was also <1 s, highlighting a critical time interval in which animals can successfully address one another. This result fits with those of Nakahara and Miyazaki (2011) who showed that countercalling between pairs of bottlenose dolphins occurred in <1 s time intervals.

The tight temporal sequencing of vocal interactions may allow animals to recognize a reply versus an independent call, thereby providing members of a communication network with a way to mediate social interactions. The identification of individual dolphins is greatly enhanced by their highly individualized signature whistles. The matching of these whistles, whereby a vocal response is reliably elicited, allows animals to localize or initiate interactions with other individuals with whom they specifically want to associate. The matching of calls has also been described in other odontocete species such as killer whales, *Orcinus orca*, and sperm whales, *Physeter macrocephalus* (Miller et al., 2004; Schulz et al., 2008), although these calls were not individual identifiers but

group calls. In these instances vocal matching is believed to play a role in coordinating movement and strengthening social bonds.

In songbirds, the necessity to establish and maintain territory boundaries has led to the use of matching as a form of contest escalation (Searcy & Beecher, 2009). Song type matching in male songbirds has long been established as an agonistic signal that occurs between both neighbours and strangers (Beecher et al., 2000; Burt et al., 2001). Although our subjects showed high levels of interest to the playback speaker, irrespective of playback type, there was no evidence that matching induced aggressive states. We found no differences in the behaviour of the target animals between the two playback treatments. Many of the animals approached the speaker and stayed within 3 m of it. Although a key measure of aggressive response in songbirds is close approach and continued proximity to the speaker (Beecher et al., 2000; Krebs, Ashcroft, & Van Orsdol, 1981; McGregor et al., 1983), bottlenose dolphins are not territorial and are not under the same social pressures as songbirds. The close approach or continued proximity of conspecifics is not a known sign of aggression in bottlenose dolphins. Instead, aggression is aligned with other signals such as an increased production of burst-pulsed sounds, jaw popping (Overstrom, 1983) or increased swim speed. The bottlenose dolphins in this study did not engage in these behaviours but nearly always responded to being matched by calling back with the same call (their own signature whistle); this was true for adult males, adult females and young calves. As such it is unlikely that reciprocating the match in dolphins has an agonistic role, but instead appears to serve an affiliative function, supporting our previous findings (King et al., 2013).

Wild conures also match specific acoustic properties of one another's 'chee' calls in vocal interactions (Balsby & Bradbury, 2009). It is difficult to tease apart the signal value of matching in conures, as they do not consistently respond with convergent call types (Balsby & Bradbury, 2009). Instead, convergent, divergent and variable patterns of call type similarity are observed in response to 'chee' call playbacks (Balsby & Bradbury, 2009). There does, however, appear to be a differential response by sex whereby males preferentially reply to convergent 'chee' calls and females reply to both convergent and divergent calls (Balsby & Scarl, 2008). The fact that both sexes respond to convergent calls in a non-agonistic context suggests it has an affiliative function (Balsby & Scarl, 2008) that may facilitate the addressing of individuals (Balsby et al., 2012). There are also more subtle forms of vocal matching, with some primate species matching fine-scale features of a call type when calling together as a means of social affiliation (Mitani & Brandt, 1994; Sugiura, 1998) or to promote partner preferences (Biben et al., 1986). We did not find that dolphins adjusted fine-scale parameters of their signature whistles as a result of being matched. It therefore seems unlikely, at least in this context, that additional information is encoded within the whistle pertaining to a change in the animal's motivational state, but rather the response in itself is strong indication of the animal's motivation to communicate.

For matching with learned signals to occur animals may have to possess some knowledge of the acoustic model they wish to match. Male songbirds must share at least some of their song repertoire in order to partake in song type matching (Searcy & Beecher, 2009). Individual bottlenose dolphins, however, use a learned signature whistle as a signal of identity (Caldwell & Caldwell, 1965; Caldwell et al., 1990; Janik et al., 2006). Signature whistle matching can therefore only occur if an animal copies the signature whistle of another animal. We know dolphins can produce copies of novel acoustic signals after only one exposure (Richards et al., 1984), and therefore it is likely that they are able to copy the signature whistle of a stranger. So far, however, signature whistle copying has been

Table 2

The behavioural response to the two playback treatments by six animals: own signature whistle (match, $N = 35$) and different signature whistles (control, $N = 27$)

	Playback treatment	
	Match	Control
Component 1	0.13±0.32	−0.17±0.35
<i>P</i>		0.3
Component 2	−0.18±0.19	0.23±0.19
<i>P</i>		0.2

The principal component scores (mean ± SE) for the first two components are given (component 1: which pool the animal spent most time in; component 2: distance to the speaker). The *P* value is for a two-tailed Wilcoxon rank sum test.

shown to occur among closely bonded animals, and these copies may even contain information on the copier's identity (King et al., 2013). Thus it is unlikely that signature whistle matching would occur between animals that do not associate together. Selective pressure on the maintenance of individually specific bonds in the dolphin's dynamic social system has probably led to signature whistle matching being used to strengthen social relationships and facilitate localization of specific animals in large social networks.

Finally, birdsong has long been acknowledged as an influential model system to address evolutionary questions on vocal learning and complex vocal communication (Catchpole & Slater, 2008). Vocal learning has been discussed as a prerequisite for the evolution of spoken language (Fitch, 2005), and is important in both the development of birdsong (Catchpole & Slater, 2008) and the ontogeny of signature whistles (Fripp et al., 2005; Miksis, Tyack, & Buck, 2002; Tyack & Sayigh, 1997). Both songbirds and dolphins are also highly sophisticated at vocal imitation (Catchpole & Slater, 2008; Richards et al., 1984). The rapid copying of signals occurs in vocal matching interactions in species from both taxa, yet in order to be an effective signal of addressing, the time between these calls must be short. We have shown that by using time intervals that are salient to the animal, signallers in open communication networks can successfully direct calls to particular receivers. Our results also highlight that vocal matching with learned signals is a universal form of addressing used in both dyadic interactions, for example birds' territorial disputes and larger communication networks such as dolphin societies. In bottlenose dolphins, vocal matching appears to be an affiliative signal between closely bonded animals; in songbirds it is a signal of aggressive intent between male territory holders. Nevertheless, species from two different taxa, which are under completely different selective pressures, have converged on a similar mechanism to address individual conspecifics using learned signals. The copying of learned signals, as a way of addressing social companions, is ubiquitous in human society. The striking parallel between nonhuman taxa presented here may therefore also provide a significant contribution to our understanding of the roots of human language evolution.

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APPENDIX 1

Swim speed was based on a four-point index, which differed between the two facilities. At the Seas: 1 (still), 2 (slow circling: >12 s spent each side of the pool), 3 (circling: 6–12 s each side of the pool), and 4 (fast swimming: <6 s each side of the pool and

splashes/tail slaps). At Dolphin Quest: 1 (still), 2 (slow circling: >25 s each side of pool), 3 (circling: 8–25 s each side of pool), 4 (fast swimming, <8 s each side of pool and splashes/tail slaps). The criteria differ because of the differing pool sizes at the two facilities and were calculated to ensure the speeds measured were equalized between facilities.

APPENDIX 2

Table A1

Frequency and temporal parameters of the signature whistles of four animals before and after the match playback

	N	Before playback Mean±SD	After playback Mean±SD	P
No. of loops				
- Ranier	17	2.2±0.2	1.9±0.2	0.2
- Khyber	4	2.2±0.9	2.7±0.9	0.1
- Cirrus	16	2.7±0.7	2.8±0.5	0.8
- Bailey	6	1.8±0.4	1.4±0.5	0.3
Start frequency (kHz)				
- Ranier	17	5.3±0.4	4.4±0.2	0.08
- Khyber	4	9.8±0.9	9.4±1.8	0.7
- Cirrus	16	7.9±3.3	7.2±2.7	0.4
- Bailey	6	4.9±0.6	11.9±7.1	0.08
End frequency (kHz)				
- Ranier	17	21.4±1.1	22.1±0.6	0.5
- Khyber	4	6.8±0.9	7.4±0.3	0.2
- Cirrus	16	21.9±3.2	23.2±4.7	0.2
- Bailey	6	12.8±1.2	15.6±3.8	0.2
Minimum frequency (kHz)				
- Ranier	17	4.0±0.2	3.8±0.2	0.2
- Khyber	4	6.8±0.9	6.7±0.7	0.8
- Cirrus	16	4.3±0.4	4.2±0.3	0.8
- Bailey	6	4.3±0.6	5.6±2.0	0.2
Maximum frequency (kHz)				
- Ranier	17	21.4±1.1	22.1±0.6	0.5
- Khyber	4	13.0±0.8	13.5±0.7	0.06
- Cirrus	16	22.0±3.2	23.4±4.5	0.2
- Bailey	6	4.0±0.07	4.4±0.6	0.2
Duration (s)				
- Ranier	17	0.5±0.04	0.4±0.03	0.06
- Khyber	4	0.7±0.3	0.8±0.3	0.1
- Cirrus	16	0.9±0.2	0.8±0.1	0.1
- Bailey	6	0.8±0.2	0.6±0.2	0.03

An *F* test was used to compare variances followed by a paired *t* test. None of these tests were significant after applying a necessary Bonferroni adjustment for multiple testing. Only four of the seven animals were included in this analysis owing to small sample sizes.